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Modes of ear reduction in iguanian lizards (Reptilia, Iguania); different paths to similar ends

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Synopsis. New observations are presented on interspecific variation in ear structure in *Phrynocephalus* (Agamidae) and the Chamaeleonidae. The tympanum has probably been obscured at least fourteen times in the Iguania and more extensive ear reduction has occurred independently at least once in each of five separate clades. Combining information on ear reduction with estimated phylogenies of the groups concerned demonstrates that the process has been initiated in at least two quite different ways in the Iguania. Modifications to the ear are congruent with hypotheses of phylogeny based on other characters in *Tympanocryptis*, the *Cophotis-Lyriocephalus-Ceratophora* clade, phrynosomatid sand lizards, and to a large extent in the Chamaeleonidae. In *Phrynocephalus* there is evidence that some modifications show partial reversal in one or more lineages.

INTRODUCTION

Different lineages of organisms often evolve a number of similar traits independently, but the order in which these are assembled may often be different, even in ecological analogues, especially if the taxa concerned are not closely related (Arnold, 1994). This phenomenon of equipotentiality, where more or less the same overall condition is reached by different routes, will be demonstrated in the external and middle ear of iguanian lizards, using some new anatomical observations and recent information on the phylogeny of this assemblage. Reduction of the external and middle ears can be shown to have occurred a number of times but by at least two primary initial routes, the various changes making up the process taking place in different sequences.

Versluys (1898) and Mertens (1971) listed cases where the tympanum is obscured in the Iguania and more extensive ear reduction in the group has been surveyed by Smith (1938). More recently, Wever (1978) discussed selected instances of ear modification in greater detail and gave information on the ability of such altered organs to transmit sound. The present account corrects some errors in Smith's otherwise useful paper and describes the wide variety of previously unreported ear conditions found in the genus *Phrynocephalus* and some more modest differences among chameleons.

MATERIAL EXAMINED

Material examined forms part of the collection of the Natural History Museum, London and a list of specimens checked is deposited in the Reptile Section there.

NOMENCLATURE

Various changes in iguanian nomenclature have been suggested recently and, to avoid confusion, usage in this paper will be specified here. The use of Phrynosomatidae for what were previously informally called sceloporine iguanids (Savage, 1958), which has been put forward by Frost and Etheridge (1989), is accepted. On the other hand, these authors' use of Chamaeleonidae is not followed. They employ the name for the whole of the Acrodonta, which comprises Chamaeleonidae in its usual sense plus what has generally been called Agamidae, including the Uromastycidae (Borsuk-Bialynicka & Moody, 1984).

Moody (1980) allocated the wide range of lizards which had long usually been referred to the genus *Agama* to a number of separate genera: *Stellio*, *Agama*, *Xenagama*, *Pseudotrapelus* and *Trapelus*. This course was followed by several authors, but the name *Stellio* is unavailable (Stejneger, 1933) and the group it was used to denote by Moody is paraphyletic, comprising distinct Palaearctic and mainly African assemblages (Joger, 1991) of which the former is probably a clade and the members of the latter more closely related to such taxa as *Agama*, *Pseudotrapelus* and *Trapelus* (personal observations). Leviton, Anderson, Adler & Minton (1992) argue for the use of *Laudakia* Gray, 1845 for the Palaearctic forms, a course followed here. The more recent suggestion (Henle, 1995), that *Laudakia* should be confined to some members of this assemblage and the rest placed in *Placoderma* Blyth, 1854, requires more thorough assessment of the relationships of these lizards. The name *Acanthocercus* Fitzinger, 1843 is available for the remainder of the forms that Moody allocated to *Stellio* (see Schätti & Gasperetti, 1994; Henle, 1995; Baig & Böhme, 1997).

DISTRIBUTION OF EAR REDUCTION IN THE IGUANIA

Basic structure of the unreduced Iguanian middle ear is shown in Fig. 1. In extreme cases of reduction, the tympanic area is covered by the anterior slip of the *depressor mandibulae*, the tympanum itself is absent and the columella becomes more robust. The distal part of the extracolumella may virtually disappear while at the same time its attachments to surrounding structures are thickened and sometimes ossified. These attachments are the internal or quadrate process, connecting to the lower quadrate bone, and the dorsal process which may connect to the paroccipital process, the intercalary ligament, or both.

At least some reduction of the ear occurs within the following apparently holophyletic groups of the Iguania.

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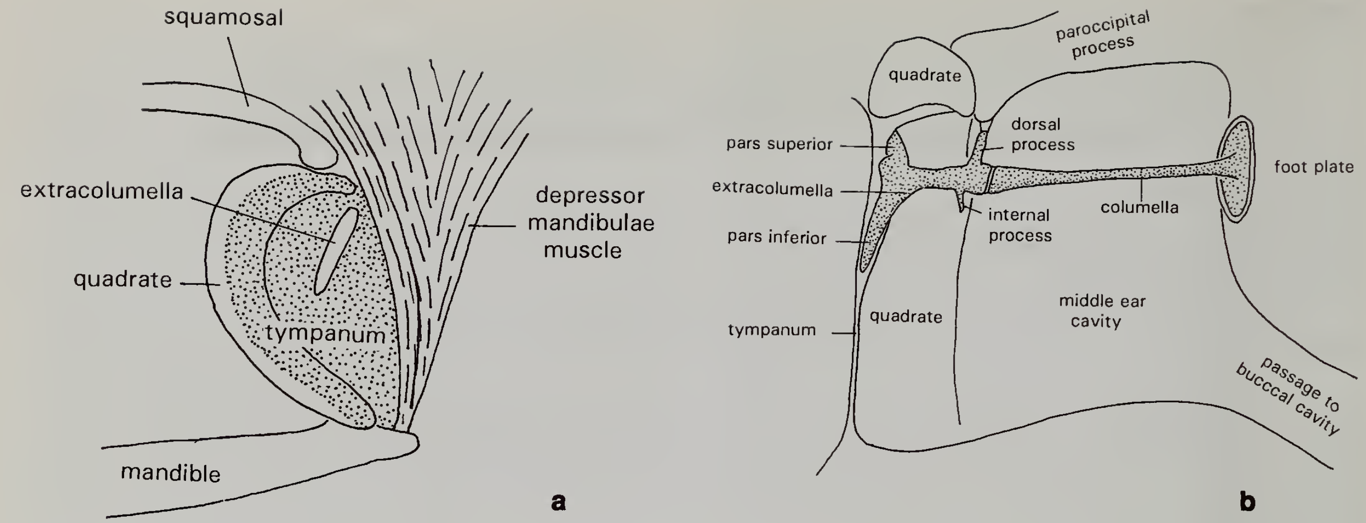

Fig. 1 General structure of the ear in Iguania. a. Lateral view of left ear, tympanum stippled. b. Transverse section of left ear. Figures based on those of Baird (1970).

Australian agamids

(Fig. 2)

Among Australian agamids of Group 3 (Moody, 1980), ear modification has occurred independently in *Ctenophorus maculosus* (Mitchell, 1948) and in all the species of *Tympanocryptis* Peters, 1863, except *T. adelaidensis* and *T. diemensis* (data from Cogger, 1992). In *Ctenophorus maculosus* and the *Tympanocryptis parviceps* Storr, 1964 group the ear is covered with scaly skin but the tympanum is present just beneath it (Greer, 1989). In the *Tympanocryptis lineata* group (species examined: *T. lineata* Peters, 1863, *T. intima* Mitchell, 1948 and *T. cephalus* Günther, 1867) further reduction has occurred. The anterior slip of the *m. depressor mandibulae*, has moved forwards beneath the skin to cover the tympanic area, the columella is more robust, no clear tympanum exists, the extracolumella is reduced to a small projection, and the dorsal and internal processes are robust and sometimes ossified. The middle ear opens broadly into the buccal cavity in *T. lineata* and *T. intima*, but more narrowly in *T. cephalus*.

Arboreal agamids of the Oriental region

(Fig. 2)

Among mainly arboreal agamids of the Oriental region which constitute Group 4 (Moody, 1980), a fully exposed tympanum is lacking in some or all members of the following apparent clades (relationships based on the weighted and unweighted Wagner tree analyses of Moody, 1980) 1. *Gonocephalus* Kaup, 1805 (partly obscured in *G. miotympanum* (Günther, 1872)); 2. *Japalura* Gray, 1853 (some species); 3. *Phoxophrys* Hubrecht, 1881, 4. *Otocryptis* Wagler, 1830; 5. *Draco* Linnaeus, 1758 (some species); 6. *Ptycholaemus* Peters, 1864; 7. *Aphionotis* Peters, 1864, *Ceratophora* Gray, 1834, *Cophotis* Peters, 1861 and *Lyriocephalus* Merrem, 1820; and 8. *Oriocalotes* Günther, 1864 (some individuals).

The tympanum consequently may have become obscured at least eight times in the Oriental assemblage (although *Phoxophrys* and *Otocryptis* could represent a single origin if reversal occurred in *Sitana*, the apparent sister group of the latter genus). In groups where members vary in the degree to which the tympanum is obscured, such as *Draco*, *Japalura* and *Oriocalotes*, it is apparent that covering of the external ear has taken place by development of scales on the tympanic surface (Fig. 5). Although most of the Oriental taxa with hidden tympana lack the extensive modifications found in some *Tympanocryptis*, there may be less extreme changes. *Draco* for instance has a thick columella, the stem of the extracolumella is angled relative to this, and the air-filled space in the middle ear is restricted; there is also a substantial loss of sensitivity (Wever, 1978)

Only in the clade made up of *Aphaniotis*, *Cophotis*, *Lyriocephalus* and *Ceratophora* has the process of ear modification gone further. The relationships of this group (based on Moody, 1980) are shown in Fig. 2. In this assemblage, the basal *Aphionotis* has the tympanum covered (Fig. 5c), but little other change is apparent, apart from the columella being robust and the exposure of the extracolumella on the tympanum large (checked in *A. acutirostris* Modigliani, 1889, *A. fusca* (Peters, 1864) and *A. ornata* Lidth de Jeude, 1893). In the sister genera *Cophotis* and *Lyriocephalus*, the tympanum has disappeared and this area is covered by the anterior slip of the *m. depressor mandibulae.* The pars superior of the extracolumella is absent, the pars inferior is small and projects laterally, and the dorsal and internal processes are robust and ossified, the former attaching substantially to the paroccipital process. The quadrate itself is more or less straight and without an auditory cup, while the middle ear cavity extends laterally as far as the tympanic area and has a quite large opening to the buccal cavity. In *Ceratophora*, the ear is essentially similar (illustrated by Wever, 1978) but there are no openings from the buccal cavity to a distinct middle ear cavity (checked on *C. aspera* Günther, 1864, *C. stoddarti* Gray, 1834 and *C. tennentii* Günther, 1861).

Smith (1938) erroneously attributed a highly modified middle ear structure to *Aphaniotis* and also incorrectly described the middle ear openings to the buccal cavity of this genus, *Cophotis* and *Lyriocephalus* as being strongly reduced.

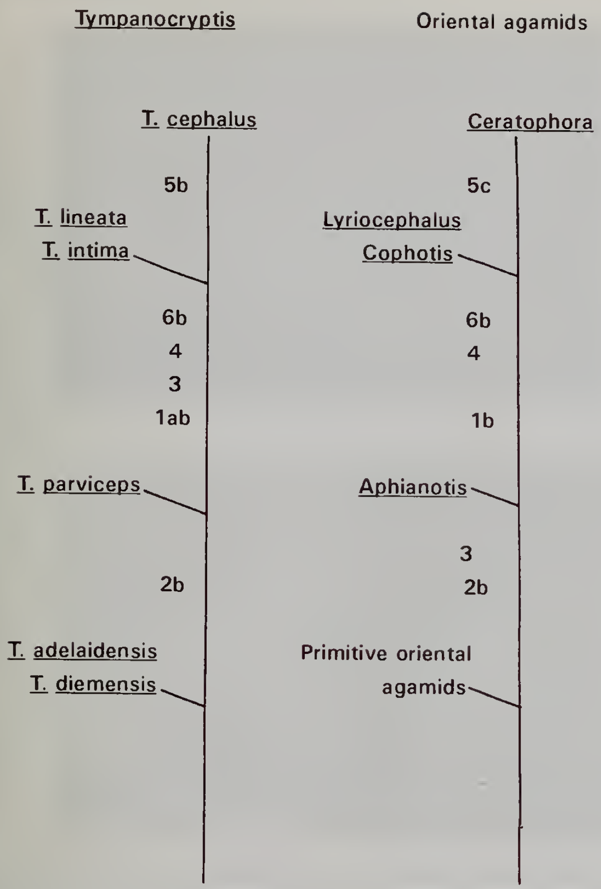

Fig. 2 Pattern of ear reduction in *Tympanocryptis* (Agamidae). and in the clade made up of *Aphaniotis*, *Lyriocephalus*, *Cophotis* and *Ceratophora* (Agamidae).

Abbreviations: 1. depressor mandibulae moves forwards, a - slightly, b. extensively. 2. Tympanum covered, largely -a, entirely - b; 3. columella robust. 4. tympanum disappears. 5. buccal opening to the middle ear reduced, a - somewhat, b - strongly, c - very small or absent. 6. Pars inferior of extracolumella reduced, a - somewhat, b - strongly or absent.

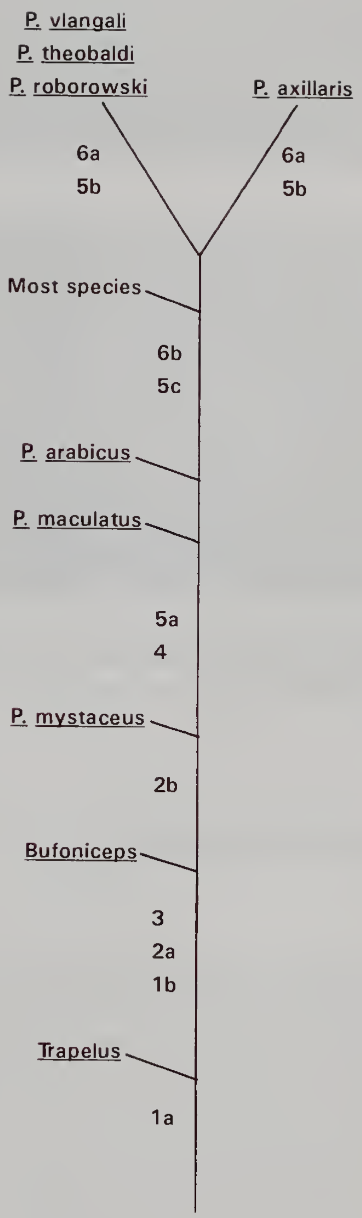

Fig. 3 Pattern of ear reduction in *Phrynocephalus* and its relatives (Agamidae). For abbreviations see Fig. 2.

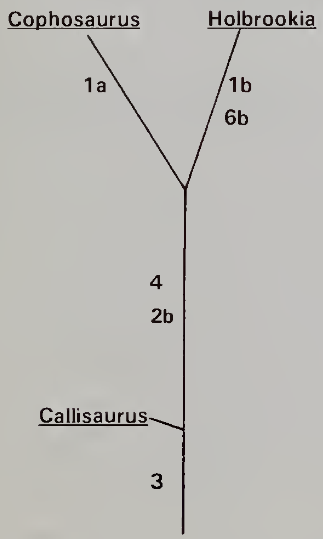

Fig. 4 Pattern of ear reduction in phrynosomatid sand lizards (Phrynosomatidae). For abbreviations see Fig. 2.

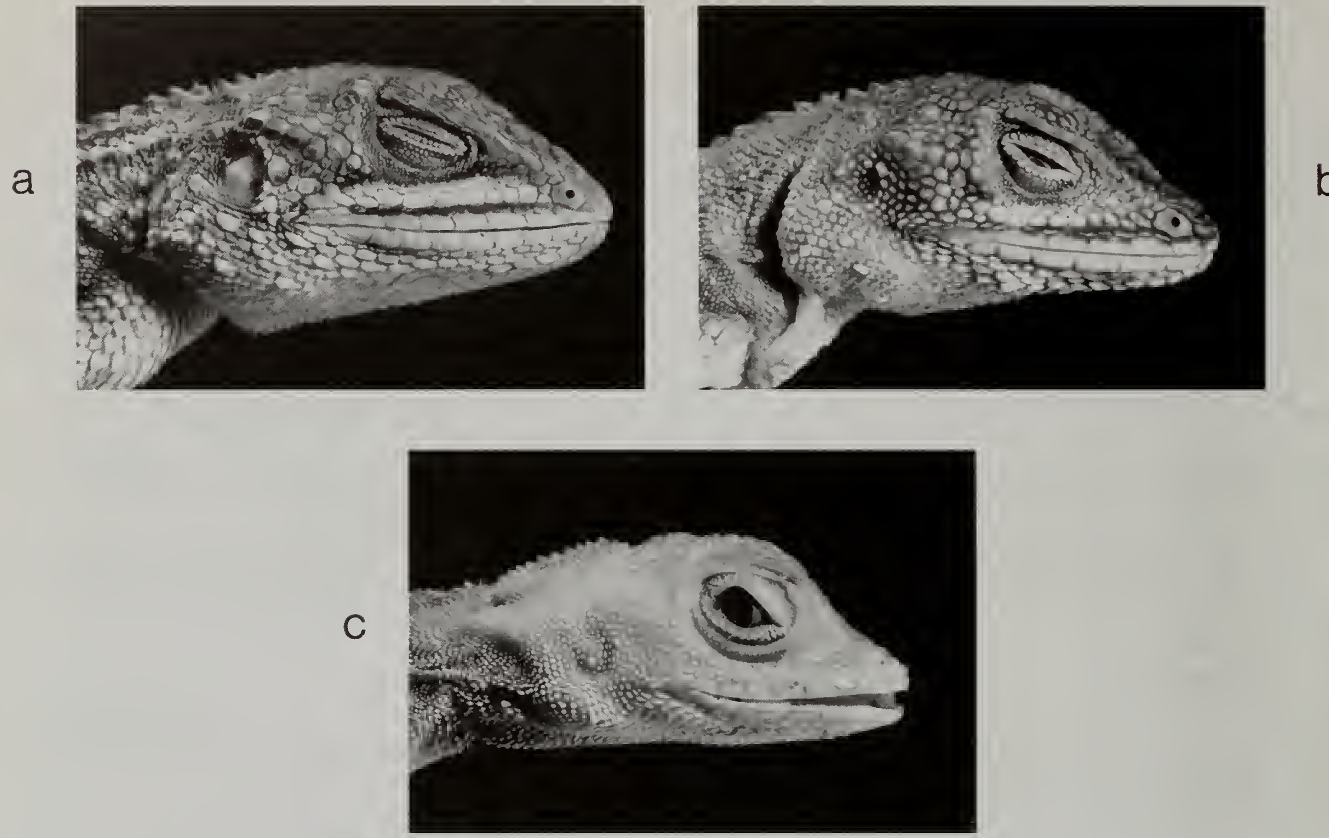

Fig. 5 Stages in reduction of the external ear in Oriental agamids. a. Tympanum superficial and exposed, *Japalura dymondi*, BMNH 1914.3.2.2.; tympanum indicated by a depression but covered with scales, *Japalura polgyonata ishikagiensis*, BMNH 1913.3.10.9; tympanic area scarcely sunk and covered with unmodified skin, *Aphaniotis fusca*, BMNH 1886.12.28.12–13.

Phrynocephalus and its relatives

(Fig. 3)

Moody (1980), on the basis of his morphological study of the Agamidae, regarded *Phrynocephalus* as the sister group of *Laudakia* plus *Acanthocercus* and a relationship to *Laudakia* has also been supported by immunological evidence (Joger, 1991). However, a more detailed anatomical investigation (in progress) suggests that *Phrynocephalus* is the sister group of *Bufoniceps* Arnold, 1992 (a new generic allocation for *Phrynocephalus laungwalaensis* Sharma, 1978) and successively more distant relatives are *Trapelus*, *Pseudotrapelus*, various African taxa the relationships of which are yet to be fully resolved including *Agama*, *Xenagama* and species assigned to *Acanthocercus*, and then *Laudakia* (Fig. 3) This hypothesis of relationships is used in the following reconstruction of the history of ear reduction in the group. However, even if *Phrynocephalus* plus *Bufoniceps* is regarded as the sister group of *Laudakia*, only evidence for the initial changes in stage 1 below would be lost.

An estimate of *Phrynocephalus* phylogeny based on morphology (Arnold, 1999) suggests that successive branches on the main lineage are: *P. mystaceus*; *P. maculatus*; *P. arabicus*; the *P. interscapularis* group (*P. interscapularis*, *P. sogdianus*, *P. ornatus*, *P. clarkorum*, *P. luteoguttatus* and *P. euptilopus*); *P. scutellatus*; *P. golubevi*: *P. reticulatus*; *P. raddei*; there is then a large clade made up of most of the remaining species. Within the latter assemblage, little robust phylogenetic structure is apparent but *P. roborowski*, *P. theobaldi* and *P. vlangali* are clearly closely related to each other and perhaps more distantly to *P. forsythi*.

1. In some *Trapelus*, the anterior slip of the *m. depressor mandibulae* moves anteriorly to partly obscure the tympanum, producing a short meatus with a small opening (Fig. 6b; at the same time the bar-like, superficial part of the extracolumella becomes more horizontal.
2. In *Bufoniceps*, the tympanum is directed more posteriorly, the *m. depressor mandibulae* moves further forward and the meatus and its surface opening become very narrow (Fig. 6c), so that its depth is several times the width of the latter.
3. In all *Phrynocephalus*, the tympanic area is entirely covered by skin (Fig. 6d) and substantially by the *m. depressor mandibulae.* In *P. mystaceus*, there is still a well defined tympanum incorporating a extracolumella which lacks the pars superior, but the pars inferior is large and overlaps the conch of the quadrate. The dorsal process is long and joins the intercalary cartilage, and the internal process is quite slender. The buccal opening to the middle ear is large and extends from the back of the basisphenoid process well beyond the spheno-occipital tubercle of the basioccipital bone; its greatest dimension is over 25% of the head length in small specimens.

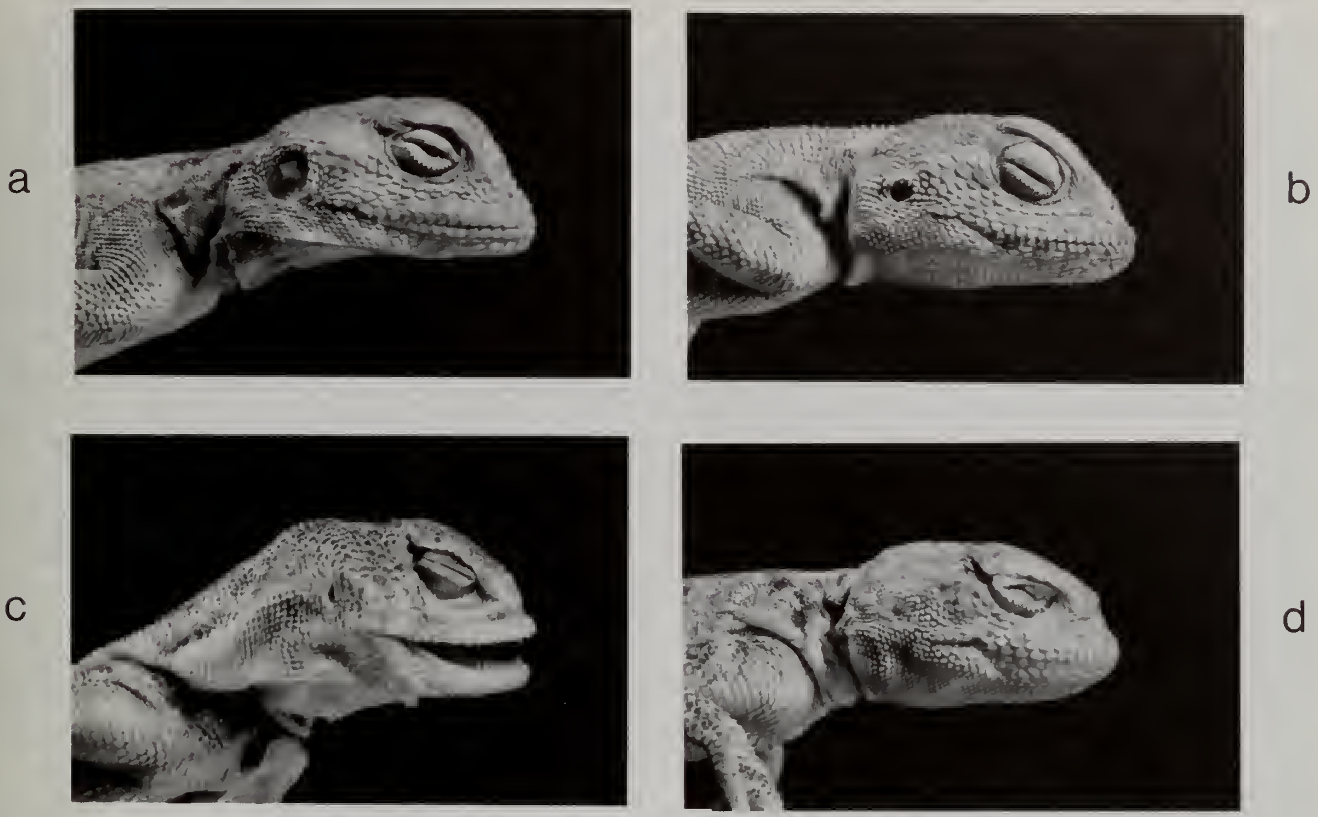

Fig. 6 Stages in reduction of external ear in the clade containing *Phrynocephalus*. a. Tympanum superficial and fully exposed, *Pseudotrapelus sinaitus* (BMNH 1953.1.7.9); b. tympanum sunk and external opening of meatus so formed reduced, *Trapelus agilis* (BMNH 94.11.13.4); c. tympanum deeply sunk and meatus and external opening very narrow, *Bufoniceps laungwalaensis* (BMNH 1975.1592); d. meatus totally closed *Phrynocephalus maculatus* (BMNH 1973.2038).

4. In *P. maculatus* the tympanum is reduced to a delicate membrane and, while smaller than in *P. mystaceus*, the extracolumella still overlies the quadrate; the buccal opening to the middle ear is reduced in size, its greatest dimension being about 15–20% of the head length. *P. arabicus* is similar but the buccal opening is rather smaller.
5. In most of the other species of *Phrynocephalus* which form a large terminal clade, the extracolumella is very small or absent and, if present, does not overlap the quadrate or only slightly. The buccal opening to the middle ear is also minute or absent.
6. The only exceptions to this arrangement within the large terminal clade of *Phrynocephalus* are *P. roborowski*, *P. theobaldi*, *P. vlangali* and *P. axillaris*. These are generally similar to *P. maculatus* and *P. arabicus*, but the entrance to the middle ear is smaller, not extending beyond the spheno-occipital tubercle of the basi-occipital bone, the greatest dimension being about 10–14% of the head length. Relationships within *Phrynocephalus* suggest that the condition found in these species results from evolutionary reversal with the extracolumella increasing in size and the buccal entrance of the middle ear re-evolving or at least enlarging. Reversal may have occurred twice: in the common ancestor of the first three species and perhaps independently in *P. axillaris*.

Some variation also exists within *Phrynocephalus* in the extent to which the anterior slip of the m. depressor mandibulae extends over the quadrate bone and whether the dorsal and internal processes are ossified, although this does not constitute a regular phylogenetic pattern.

Chameleons

In chameleons, the skin over the quadrate region is more or less like that covering surrounding areas, the tympanum has disappeared and the *m. depressor mandibulae* runs close to the quadrate which is straight; the columella is short, and the extracolumella elongate, with a superior ligament attached to it.

Variation exists, for instance in the form of the pars inferior of the extracolumella and the extent to which this is embedded in the *m. depressor mandibulae* (Wever, 1968). There is an anterior process extending to the flattened posterior section of the pterygoid in *Chamaeleo quilenis* Bocage, 1866. *C. senegalensis* Daudin, 1802 and *C. chamaeleon* (Linnaeus, 1758) (Wever, 1978) and in *C. dilepis* Leach, 1819 and *Bradypodion ventrale* (Gray, 1845) (personal observations). This is lacking in *Chamaeleo elliotti* Günther, 1895, *C. fischeri tavetanus* Steindachner, 1891, *C. hoehnelii* Steindachner, 1891 and *C. jacksoni* Boulenger, 1896 (Wever, 1968), in the Madagascan *C. brevicornis* Günther, 1879 and *C. lateralis* Gray, 1831 (referred to *Calumma* Gray, 1865 and *Furcifer* Fitzinger, 1843 respectively by Klaver & Böhme, 1986), and in the dwarf *Rhampholeon brevicaudata* (Matschie, 1892) and *Brookesia stumpfii* Böttger, 1894 (personal observations).

Among the same species, the African forms assigned to *Chamaeleo* Laurenti, 1763 have small but well developed buccal openings into the middle ear, but these are less obvious although present in the two large Madagascan forms examined. In *Bradypodion ventrale* there are indentations where the openings would normally be but the openings themselves are absent. This also true of the *Rhampholeon* Günther, 1874 and *Brookesia* Gray 1865 studied in which there are not even indentations.

Ear reduction in the Phrynosomatidae

(Fig. 4)

Relationships within the Phrynosomatidae are discussed by De Queiroz (1992) and ear structure of various members of the group is described by Earle (1961a, b, c; 1962), Wever(1978) and Montanucci (1987).

In *Phrynosoma* there is stiff skin over the tympanum and sometimes this is very like that surrounding it, but middle ear structure is basically normal. *Uma* has an essentially unmodified ear, but in *Callisaurus* the columella is more robust and contacts the inner edge of the quadrate bone, while the extracolumella is more heavily built, directed backwards and has much stronger dorsal and internal processes; the quadrate is also somewhat modified. In *Holbrookia* and *Cophosaurus*, there is no ear opening, the tympanum is absent and the columella is even more robust attaching to the quadrate via a short, broad internal process. *Cophosaurus* has the tympanic area partly covered by the *m. depressor mandibulae* and the quadrate is more or less straight instead of cup-shaped. In *Holbrookia*, the extracolumella is very reduced, covering of the tympanum by muscles is greater than in *Cophosaurus* but modification of the quadrate rather less.

PATTERNS OF MODIFICATION

In summary, a limited degree of external and middle ear reduction, including covering of the tympanum by unmodified skin, has probably occurred at least fourteen times in the Iguania. More extensive modification has taken place in *Tympanocryptis*, the *Cophotis-Lyriocephalus-Ceratophora* clade, *Phrynocephalus*, the Chamaeleonidae and the *Callisaurus-Holbrookia-Cophosaurus* clade. In all these groups, different species exhibit markedly different degrees of modification. When these varied conditions are plotted on phylogenies of the groups concerned (Figs 2–4), it is possible to get some idea of the order in which particular features of the modified ears appeared. To be able to reconstruct a complete sequence on a lineage, the origin of each new feature must be separated from those of others by side-branches, otherwise, reconstruction will be impossible or incomplete (Arnold, 1994). In the Chamaeleonidae only two basic degrees of modification exist and only three in *Tympanocryptis*, in *Aphionotis-Cophotis-Lyriocephalus-Ceratophora*, and in *Callisaurus-Holbrookia-Cophosaurus*. In the clade containing *Phrynocephalus*, on the other hand, there are at least six successive conditions.

It is apparent that the sequence of ear modification has been different in some groups even though the end results have substantial similarity. Thus, In the Oriental agamids, and *Ctenophorus* and *Tympanocryptis*, the tympanum was first obscured by becoming scaly (Fig. 5) and only then did other changes take place, such as the *m. depressor mandibulae* moving forwards to cover the tympanic area and the columella becoming more robust. In contrast, more basal members of the clade containing *Phrynocephalus* show that movement of the *depressor mandibulae* muscle took place first, creating and then narrowing a meatus (Fig. 6) and it was only when this process was complete that the tympanum was entirely cut off from external contact. In phrynosomatids, the earliest change involved the columella and extracolumella becoming more robust, rather than the tympanum becoming obscured. Complete closure of the buccal opening is the final stage in the groups where it occurs but, in the *Callisaurus-Holbrookia-Cophosaurus* clade, has not taken place, even though the ear is otherwise highly modified.

The reasons for the extensive ear modification found in some iguanians are uncertain. The ground-dwelling forms that exhibit these conditions occur in arid areas and many of them burrow directly into loose sand or earth. In this situation, covering or modifying the primitively delicate tympanum and associated middle ear structures may protect them from damage. Again, a more robust columella with direct attachment to the quadrate may be more efficient at transmitting low amplitude vibrations generated on or in the substrate by predators, prey or conspecifics. Ability to detect such vibrations sometimes has clear benefits, for instance in the sand-burrowing *Scincus scincus* (Hetherington, 1989). However these possible performance advantages seem unlikely to apply to the various tree dwelling forms that exhibit reduction of the external and middle ears. It might be expected that the differences, in the order in which specific modifications of the ear appear, result from different selective regimes or different sequences of these. However, differences in order of modification even occur between ground-dwelling forms, in which selective regimes are likely to be similar.

USE OF THE OUTER AND MIDDLE EARS IN THE SYSTEMATICS OF THE IGUANIA

Although loss and reduction features are often said to be of low value in phylogeny reconstruction (see for instance Hecht and Edwards, 1977), changes in the outer and middle ear of the Iguania do not always fit this preconception. Obscuring of the tympanum has occurred many times, but loss of more structure is often congruent with changes in other characters within groups. Thus ear alterations do not conflict with phylogenies based on other features in *Tympanocryptis*, the *Aphaniotis-Cophotis-Lyriocepalus-Ceratophora* clade and in the phrynosomatid sand-lizard group. Similarly, there is some congruence with classifications of chameleons based on lung and hemipenial structure (Klaver & Böhme, 1986). For instance within *Chamaeleo* the development of a pterygoid connection to the columella is confined to the subgenus *Chamaeleo*. However, loss of a buccal opening to the middle ear occurs in the *Brookesia-Rhampholeon* group but is also found in *Bradypodion* which may be more closely related to other larger chameleons (Klaver & Böhme, 1986). Although many changes in the ear on the *Phrynocephalus* lineage are congruent with the phylogeny, this group is exceptional in showing reversal in some ear features.

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